Effects of climate change on the breeding success of White-fronted Geese *Anser albifrons flavirostris* in west Greenland

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Abstract

Numbers of Greenland White-fronted Goose *Anser albifrons flavirostris* pairs breeding successfully have been falling since the 1980s, markedly so since the mid-1990s. The latter change coincides with a switch in the Atlantic Multidecadal Oscillation, associated with increased spring precipitation in west Greenland. During the 1960s to 1980s, breeding success amongst birds wintering on Islay, southwest Scotland, correlated positively with summer temperatures and negatively with spring precipitation. Since 1995, poor reproduction amongst Islay-wintering birds has coincided with increased spring precipitation in the relatively dry interior of west Greenland, where many of these geese nest, and no longer shows any correlation with summer temperature. For geese wintering at Wexford, southeast Ireland, there was also a correlation between reproductive success and summer temperature prior to 1995 and no such relationship afterwards. Although this group of birds similarly shows a negative relationship between reproductive output and the more recent heavy spring precipitation since 1995, this fitness measure amongst Wexford-wintering geese is much lower now than in pre-1995 years, suggesting that factors other than climate have contributed to consistently low reproductive success. Interactions from increasing numbers of Canada Geese breeding and moulting in west Greenland offer one plausible explanation for this phenomenon, but at present there is a lack clear of evidence for this. The recent climate-related changes in the size and success of this population have been incremental. Accelerating melting of the inland ice will lead to substantial increases in the area of the interior lowlands of west Greenland and to changes in the extent and quality of the habitats used by geese that may in the long term be beneficial.

Key words: *Anser albifrons flavirostris*, arctic, *Branta canadensis*, Canada Goose, competition, Greenland White-fronted Goose, precipitation, spring condition.

White-fronted Geese breeding in mid-west Greenland form one of the smallest reproductively isolated groups of this nearly circumpolar species (Fox & Stroud 2002; Kear 2005; Ely *et al.* 2005). The rise and fall of their numbers from 14,000–16,000 since the late 1970s have been described in detail by Fox *et al.* (2006). Most recent changes result directly from a continuing decline in annual recruitment, which now fails to replace normal annual losses, and which explains the 30% fall in total numbers since the peak of 35,600 in 1999.

The Wexford Slobs, the principal Irish wintering site for the geese, has been a nature reserve for many years. On Islay, their main Scottish haunt, many of their roosting and some feeding areas are also protected and the island is the subject of a major goose management scheme. From 1982/83 onwards, prohibition of hunting of White-fronted Geese throughout their winter quarters helped the population to grow at a rate which suggested that winter hunting mortality was completely additive (Fox 2003). Shooting of these geese in Iceland, where they spend several weeks in autumn and spring was also banned in 2006, by which time more than 3,400 were being shot annually. Hunting continues in Greenland, though fewer than 200 birds are thought to be taken there each summer (Christian Glahder, pers. comm.). It therefore seems reasonable to assume that the population has received the benefit of as much direct conservation action as possible in response to falling numbers in the 1960s, actions which have continued to the present day. So why the recent sustained decline?

Reproductive success in this population is positively correlated with summer temperatures (Boyd 1982; Zöckler & Lysenko 2000), so the poor breeding performance could perhaps be due to cooler conditions in recent years. In fact, temperatures in west Greenland, after falling steadily since the 1940s, have increased by *c.* 2°C since the late 1990s (Vinther *et al.* 2006). Potentially that should have enhanced the successful production of young. However, if the geese have to wait for many days after arrival before widespread snowmelt enables them to feed freely, the reserves of energy they brought with them from Iceland and the wintering grounds will be depleted, reducing their chances of breeding successfully. Previous studies of other goose populations have demonstrated that breeding phenology (timing of arrival, date of breeding) and reproductive success (proportion of breeding birds, brood size and the subsequent survival of the young) are related to environmental conditions on arrival on the breeding grounds, especially spring temperatures (positive correlations), precipitation and snow cover (both negative correlates) (Kostin & Mooij 1995; Bêty *et al.* 2003; Reed *et al.* 2004). Indeed, according to Kostin & Mooij (1995), snow melt must be sufficiently advanced to permit Red-breasted Geese *Branta ruficollis* to start breeding within 14 days of arrival to breeding areas, otherwise they leave the area for remote moulting sites and abandon nesting attempts altogether. Regardless of summer conditions therefore, winter and especially spring snow on arrival may have a detrimental effect on breeding success.

North Atlantic sea surface temperatures show a 65–80 year cycle, known as the Atlantic Multidecadal Oscillation (AMO) (Kerr 2000; Enfield *et al.* 2001), with warm phases during 1860–1880 and 1940–1960, and cool phases during 1905–1925 and 1970–1990. Since 1995, the AMO has reverted to a warm phase, associated with the passage of more frequent frontal systems, especially in spring across the west coast of Greenland, where White-fronted Geese breed (Sutton & Hodson 2005). This has particular consequences for the maintenance or accumulation of reserves for investment in eggs amongst breeding females, as most spring precipitation falls as snow in April and well into May. The recent increases in spring precipitation since 1995 may therefore offset any advantage of earlier arrival in west Greenland in recent years.

This paper examines whether the change in the AMO has been associated with changes in spring precipitation in west Greenland and tests the hypothesis that these changes correlate with patterns of reproduction. Specifically, two predictions are tested that might be expected if these changes in climate were responsible for changes in reproductive output in the population. First, if spring snowfall now plays a dominant role in limiting reproduction, we would expect correlations between reproductive output and warm summers to have weakened since 1995. Second, we would expect there to be a continuing inverse relationship between spring precipitation and reproductive output amongst Greenland White-fronted Geese. Finally, these findings are considered in the light of alternative potential explanations for the present unfavourable conservation status of the population.

Materials and methods

Abundance and breeding success of geese

Regular winter counts are available since the 1960s from the two most numerically important wintering areas where >60% of the population winters: Wexford Slobs (southeast Ireland) and Islay (southwest Scotland). Annual sampling of the percentages of juveniles and the mean brood sizes present is undertaken at both resorts and at two major resorts on the Mull of Kintyre in southwest Scotland (the latter available since 1982 only). These four sites hold around 75% of the world population, so these measures of reproductive success provide a reasonable measure of that of the whole population. Mean percentage young samples from the population were arcsine square root transformed before comparisons using student's t-tests. Several measures of reproductive success were calculated. First, for the wintering birds at Wexford and Islay, the percentage of young in the population (j) was estimated, expressed as the number of first winter birds (s) judged on plumage characteristics (Cramp & Simmons 1977) in the sample aged (n):

$$j = (s*100)/n$$

The number of young (J) at each resort was then estimated, based on N, the maximum winter count, as

$$J = (j/100)*N$$

The number of adults (A) each year is thus:

$$A = N - J$$

The number of families (F) at both resorts was calculated as the estimated total number of first winter birds divided by the mean brood size (B):

$$F = J/B$$

A crude index of potential breeders (PB) in the population in year y+1 was calculated as 80% of the number of adults in year y (to adjust for crude survival) divided by two:

$$PB_{y+1} = (0.8*A_y)/2$$

The proportion of successful pairs (*sp*) that were successful in year y+1 was then expressed as:

$$sp_{y+1} = F/PB_{y+1}$$

The number of young per potential breeder (P) was expressed as the number of first winter birds (J) in year y divided by the number of potential breeders PB_{y+1}:

$$P = J_y/ PB_{y+1}$$

Because winter hunting ceased after the winter 1981/82, we have chosen to break the time series after 1981 and again after 1995 (given the change in AMO), to test for differences on either side of these pivotal points.

Atlantic Multidecadal Oscillation

Values for the AMO Index are generated monthly by the US National Oceanic & Atmospheric Administration (Physical Sciences Division, Earth System Research Laboratory, National Oceanic & Atmospheric Administration Research, United States Department of Commerce) and are available from http://www.cdc.noaa.gov/Timeseries/AMO/. Two sets of mean index values were calculated, for April–May and for June–August, the two periods when the AMO might have a direct influence on goose reproduction, there being no significant links with values in the preceding winter.

West Greenland meteorological data

Kangerlussuaq (67°04´N, 50°42´W), formerly known as Søndre Strømfjord, is the only weather station within the main breeding range of White-fronted Geese that has provided monthly records of temperature and precipitation records over the period for which there are annual records of goose breeding success (available at: http://www.tutiempo.net/clima/Sdr_Stroemfjord/42310.htm, although lacking some data from 1971, 1972, 1975 and 1976). It is the only station in the interior lowlands of west Greenland and therefore represents the highly continental climate that predominates in the core breeding range of the population and from which the majority of the Islay-wintering Greenland White-fronted Geese derive (Boyd 1958; Kampp *et al.* 1988; Malecki *et al.* 2000). Temperature data are presented as mean values calculated from available mean daily values from June, July and August combined. Precipitation data are similarly presented as the cumulative totals of daily measurements for the months presented, based on mm of rainfall equivalent, even where the precipitation has fallen as snow. No snow cover data were available.

Results

Abundance and annual breeding success of White-fronted Geese

Although subject to considerable variance over the years, Islay and Wexford show no significant difference ($t_{32} = 0.365$, $P = 0.359$ and $t_{24} = 0.253$, $P = 0.401$) in the mean annual production of young in the period before protection on the wintering grounds compared to the period 1982–1995 inclusive immediately afterwards (Fig. 1). However, both resorts show significantly lower mean age ratios in the period 1996–2007 inclusive than in 1982–1995 ($t_{24} = 3.093$, $P = 0.003$ and $t_{24} = 5.003$, $P < 0.001$).

Because of the high variance amongst the Kintyre age ratios (some of which have small sample sizes and lack data in some years), there was a significant difference between 1982–1995 and 1996–2007 in age ratios sampled from the Rhunahaorine flock ($t_{19} = 3.152$, $P = 0.003$) but not amongst those from Machrihanish in the same time periods ($t_{18} = 1.501$, $P = 0.075$). However, the same general pattern is evident through the time series as at the two major resorts. Age sample ratios from throughout many different winter resorts confirm very similar trends in reproductive output across sites (e.g. Fox *et al.* 1998 and unpublished data).

The different measures of reproductive output were highly correlated and showed generally very similar trends. The numbers of families increased at both resorts from the 1970s onwards, but have shown a tendency to decline since the mid 1980s (Fig. 2). This pattern was mirrored in proportions of successful breeding birds and the numbers of young produced per

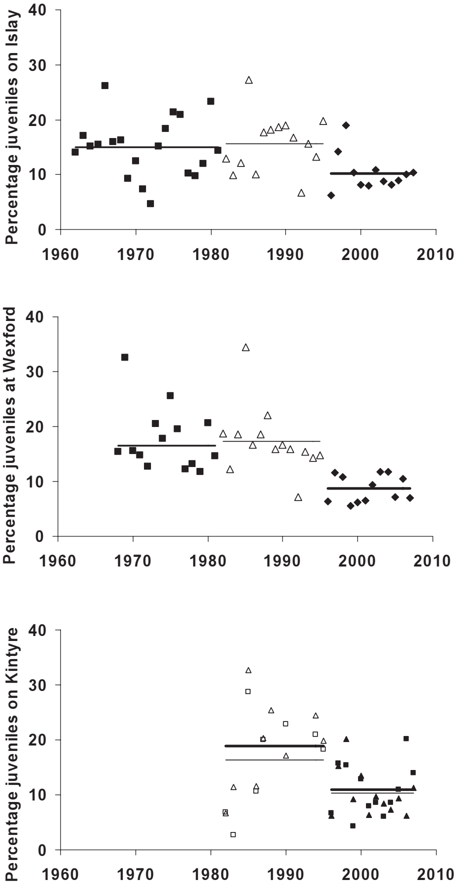

Figure 1. Annual percentage of first winter Greenland White-fronted Geese amongst samples taken on Islay, Inner Hebrides (top), Wexford Slobs, SE Ireland (middle) and the flocks at Rhunahaorine (triangles and heavy mean line) and Machrihanish (squares and lighter mean line) on the Mull of Kintyre (lower). Data from Islay and Wexford show annual values during the period up to protection in 1982 (filled squares), 1982–1995 (open triangles) and 1996–2007 (filled diamonds). Data for the Kintyre flocks are available only since 1982, but are shown for 1982–1995 (open symbols) and 1996–2007 (filled symbols). Mean values are shown as horizontal lines for each of the periods concerned.

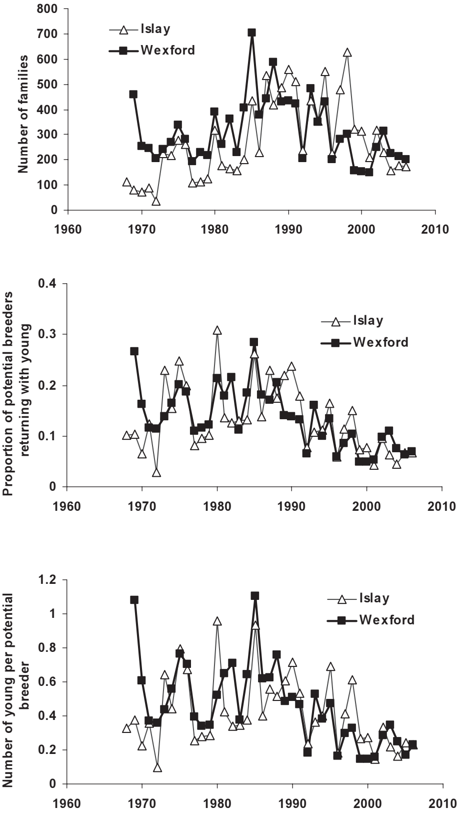

Figure 2. Long term trends in measures of reproductive output amongst Greenland White-fronted Geese wintering at Wexford Slobs and on Islay. Graphs show the number of families returning each autumn (top), the proportion of potentially breeding adults returning with young (middle) and the production of young per potentially breeding adult (lower). See text for a full explanation of the methods for estimating these measures.

potentially breeding adult (Fig. 2), both of which declined from the mid 1980s onwards. Because all of these measures show a high level of autocorrelation, we use only the percentage young assessment as an index of reproductive output in the remainder of the analysis, as all the other measures involve empirically-derived values (such as mean brood size) which are subject to additional bias and error.

Variations in seasonal weather

The annual values of the AMO are shown in Fig. 3, demonstrating the clear shift from a positive index in the 1940s until 1962, contrasting with negative values through the 1960s to 1980s, and followed by a return to positive values since 1995. Precipitation at Kangerlussuaq during the period 1968–2007, for which good goose data are available, was positively correlated with the AMO index (r = 0.33, $F_{1,39}$ = 4.72, P = 0.036). The period from 1995 onwards in particular has been characterised by the passage of more frequent low pressure frontal systems across southern parts of west Greenland which, as in previous periods of negative AMO, have brought greater winter and spring precipitation (snow) to the region and also greater annual variation in snowfall (Fig. 4).

Seasonal weather and breeding success

Over the period 1968–2007, juvenile percentages on Islay showed weak but non-significant links with summer temperatures at Kangerlussuaq (r = 0.30, $F_{1,39}$ = 3.67, P = 0.063). There was no similar relationship amongst birds at Wexford over the same period (r = 0.06, $F_{1,39}$ = 0.13, n.s.). During 1968–1995, more young geese were produced and returned to Wexford (r = 0.44, $F_{1,27}$ = 6.39, P = 0.019) and Islay (r = 0.59, $F_{1,27}$ = 14.03, P < 0.001) in years when temperatures in June–August were

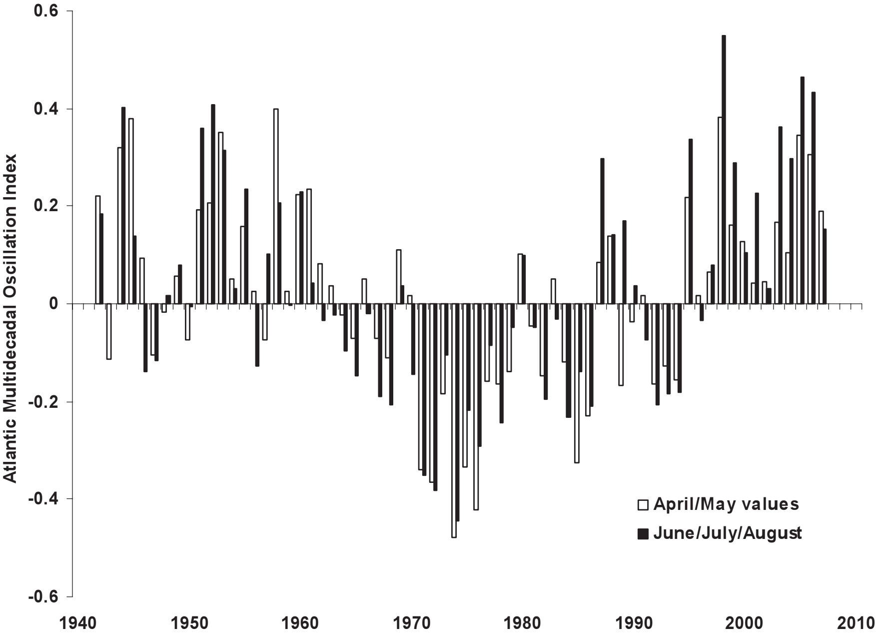

Figure 3. Annual Atlantic Multidecadal Oscillation index for April/May and June/July/August since 1942. Data points are derived from: http://www.cdc.noaa.gov/Timeseries/AMO/

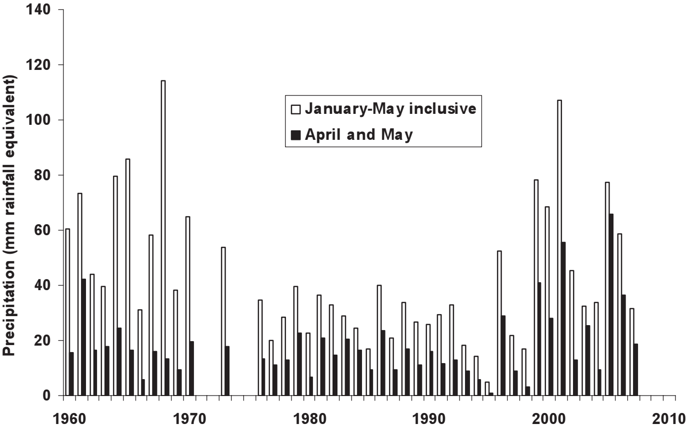

Figure 4. Annual precipitation for January–May inclusive, and also for April–May, measured at Kangerlussuaq west Greenland since 1942. Data are incomplete for 1971, 1972, 1974 and 1975; these years therefore are omitted. Note the low mean values and annual variation of the 1970s to early 1990s followed by a return to high mean values and annual variation thereafter (1996 to 2007).

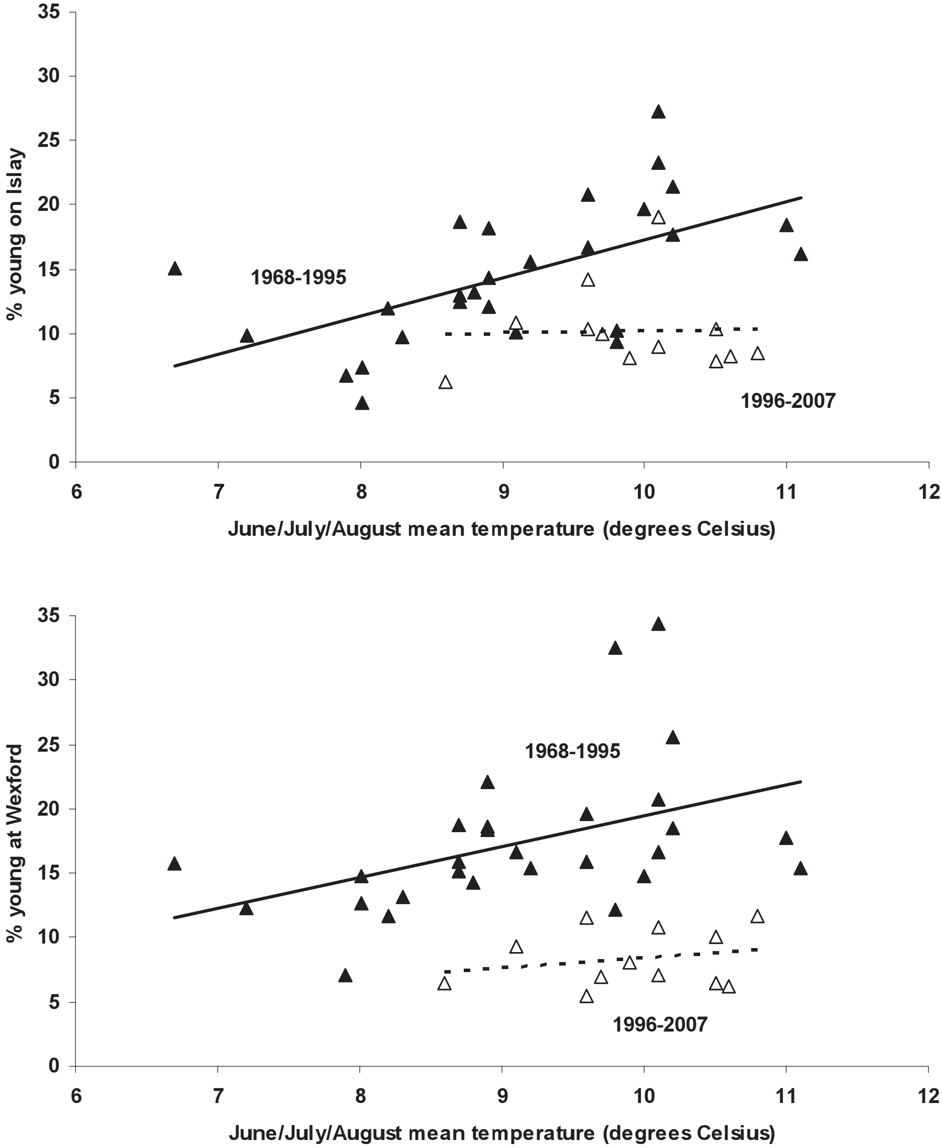

Figure 5. Annual production of young measured as percentage first winter birds in samples of Greenland White-fronted Geese wintering at Islay (upper) and at Wexford (lower), plotted against mean temperature in June, July and August of the preceding summer. Filled triangles and heavy lines denote significant fitted regression models to these datasets for the period 1968–1995; open triangles and dotted lines indicate those for the period 1996–2007, which failed to attain statistical significance (see text for full details).

relatively high (Fig. 5). During 1996–2007, no significant associations with seasonal temperatures have been apparent (Wexford $r = 0.12$, $F_{1,11} = 0.134$, n.s.; Islay $r = 0.03$, $F_{1,11} = 0.01$, n.s.; Fig. 5), but note that reproductive output has been consistently low since that time.

Over the period 1968–2007, juvenile percentages at both resorts were inversely related to April and May precipitation at Kangerlussuaq (Islay $r = 0.52$, $F_{1,36} = 12.35$, $P = 0.001$; Wexford $r = 0.48$, $F_{1,36} = 10.37$, $P = 0.003$; Fig. 6). There was no significant relationship at Wexford prior to 1995 ($r = 0.20$, $F_{1,23} = 0.90$, n.s.) but a negative one during 1996–2007 ($r = 0.67$, $F_{1,11} = 8.19$, $P = 0.017$; Fig. 6). On Islay, there was a significant inverse relationship between reproductive output and spring precipitation during 1968–1995 ($r = 0.44$, $F_{1,23} = 5.34$, $P = 0.030$) but although the tendency was clear, this failed to attain statistical significance after this period ($r = 0.52$, $F_{1,11} = 3.65$, $P = 0.085$). At both sites, the proportions of young in the samples during 1996–2007 have been significantly less than in 1968–1995 (Fig. 6).

Discussion

Several hypotheses have been proposed to explain the very low reproductive success of the Greenland race of the White-fronted Goose in recent years. These include enhanced predation, as well as several other factors that could reduce reproductive success because of the failure of the females to attain sufficient body condition for their reproductive attempt, including disease, parasites, weather and interactions with other goose species. Because of the conservation effort that has been focussed on the Greenland White-fronted Goose over many years, it is important to find evidence to support or refute the different hypotheses if the root causes for the declines are to be identified, and appropriate management actions for reversing these declines initiated.

In this analysis we considered the effects of weather on the breeding grounds as a cause of the reduced reproductive success of the population in recent years. There was little obvious change in reproductive output in the population between the early 1960s and 1995, despite the cessation of winter hunting in 1982, which had a dramatic effect on the survival and hence on the overall abundance of the population.

Since 1995, the shift in the AMO has caused more spring precipitation in west Greenland during the prelude to the arrival of the geese, across the Greenland icecap, from staging areas in Iceland used in April and early May. Arriving females are known to restore depleted stores of fat (Fox & Madsen 1981; Glahder *et al.* 1999a). Wexford-wintering geese, which breed in the north of the summer range in Greenland, also stage in more southerly parts of lowland west Greenland in early May before heading further north to breed (Glahder *et al.* 1999b; Fox *et al.* 2003). An increase in snow cover at that time is likely to cause a general delay in breeding and inhibit effective restoration of such stores, though direct evidence of this is meagre.

There was an inverse relationship between production of young amongst Islay-wintering birds and April–May precipitation

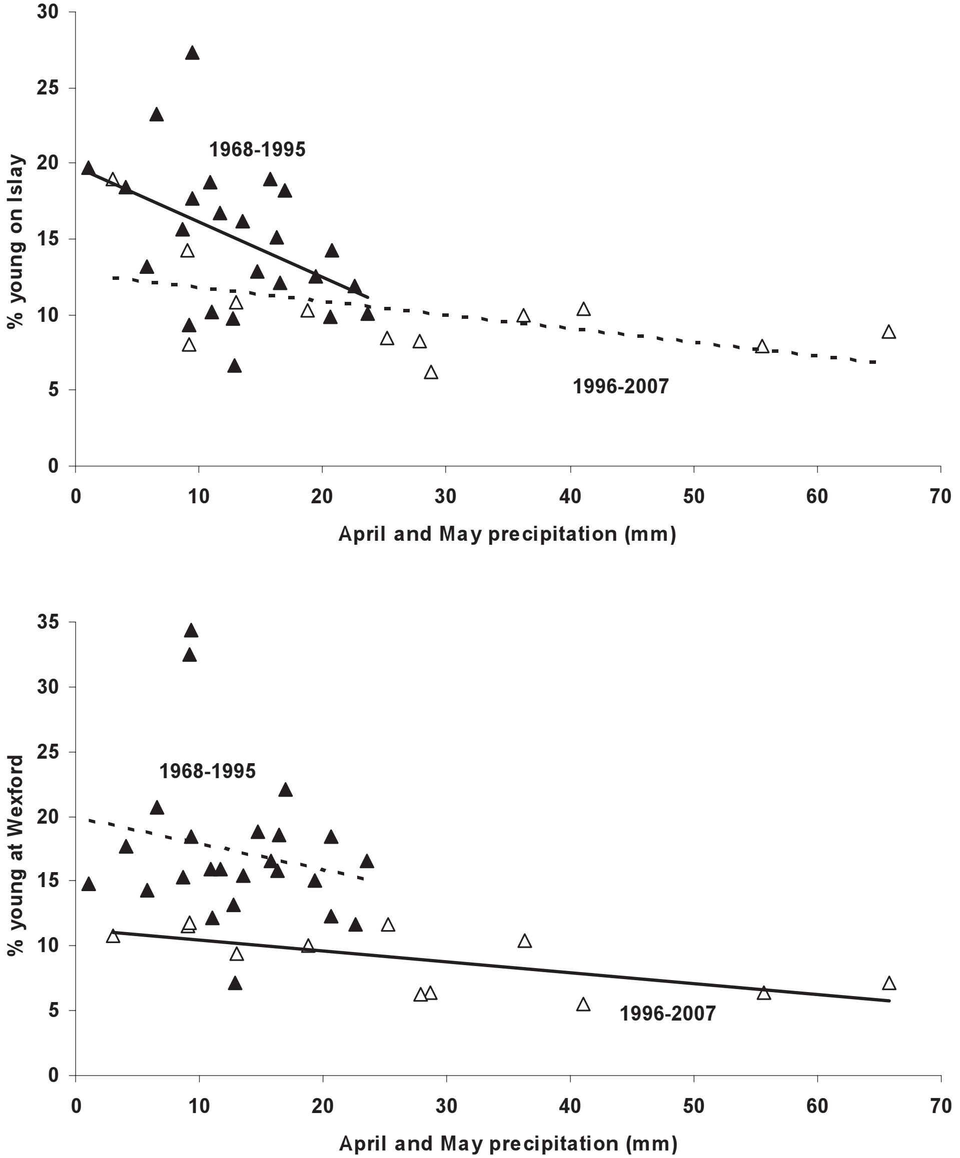

Figure 6. Annual production of young measured as percentage first winter birds in samples of Greenland White-fronted Geese wintering at Islay (upper) and at Wexford (lower), plotted against total precipitation in April and May of the preceding summer. Filled triangles indicate datasets for the period from 1968–1995; open triangles indicate those for the period 1996–2007. Solid lines denote significant fitted regressions models, dotted lines those which failed to attain statistical significance (see text for full details).

in west Greenland up to 1995 and a weak indication of such a trend amongst Wexford birds. Since 1995, there has been a tendency at both wintering resorts for inverse relationships during a phase of much heavier and variable spring precipitation (although not significant for Islay). However, reproductive success post-1995 at all wintering resorts has also been much lower after years with low spring precipitation compared with earlier years. Furthermore, Figs. 1 and 2 strongly suggest a longer term progressive decline in reproductive output, starting in the mid 1980s. The evidence therefore suggests that although low production of young is associated with high spring precipitation and formerly with low summer temperatures on the breeding areas, these are not in themselves a plausible complete explanation for the low reproductive success of recent years, suggesting that other factors may be involved.

The Greenland White-fronted Goose has always exhibited unusually low reproductive success compared to other races of the same species (Table 1). Quite why so few adults ever recruit into breeding age classes is obscure, but tracking individually marked birds showed that even in the period of expansion in the early 1980s, around 20% of goslings marked in their first winter at that time ever bred successfully (in terms of returning to the wintering quarters with at least one offspring throughout their lifetime), whilst that had fallen to less than 5% amongst cohorts hatched in the early 1990s (Fox 2003).

The proportionate breeding success of many goose populations tends to decrease as they become more numerous (see for example European White-fronted *Anser a. albifrons* and Barnacle Geese *Branta leucopsis*, although not the case for Pink-footed Geese *Anser brachyrhynchus*, Madsen *et al.* 1999). The reproductive output of Greenland White-fronted Geese has continued to decrease during an initial period of population growth and then rapid decline in recent years, suggesting mechanisms other than density dependence. The shift from traditional wetlands and low intensity agriculture to more intensive farmland as winter habitat has apparently enhanced reproductive output rather than inhibited it (Fox *et al.* 2005). Other facets of climate change may be affecting the population. Temperatures on the winter quarters have warmed by 1°C in the last 25 years, and Greenland White-fronted Geese have been departing Ireland and Scotland earlier in spring (Alyn Walsh pers. comm.) yet staging for similar durations in Iceland, where the entire population stops for 3–4 weeks (although individuals may stage for much less) before moving on to west Greenland (Fox *et al.* 2003 and unpublished data). The advances in the timing of spring migration seem to have resulted chiefly from improvement in the quality and abundance of the cultivated grasslands upon which they now predominantly feed during spring staging in Iceland. While much of that improvement is due to advances in farm technology (Humphreys 2007), increasing temperatures in winter and spring have accelerated the resumption of grass growth in Ireland (French *et al.* 2006), and in Iceland (Bergþórsson 1985; Helgadóttir & Sveinsson 2006). Warming has also occurred in west Greenland, and since Greenland

Table 1. Mean percentage of juveniles in autumn among different North American populations of White-fronted Geese, compared to those for Greenland White-fronted Geese, for the years 1983–2006. North American data are derived from Ferguson (2007).

	Number of years with data	**Mean ± s.e.**
Greenland (weighted mean)	24	13.4 ± 1.3
Mid-Continent (Canada)	20	33.2 ± 1.2
Mid-Continent (Canada)	23	25.4 ± 1.6
Tule (Alaska)	20	24.6 ± 1.3

White-fronted Geese exploit an altitudinal gradient of thaw that progressively frees their summer food supply, mismatches in timing of climate change processes on the wintering, spring staging and breeding areas may have had adverse effects on the ability of females to acquire nutrients in time to invest in egg-laying and incubation.

It seems increasingly likely that causes of poor reproductive success have arisen in Greenland and it is there that interactions with Canada Geese constitute another hazard. During the last twenty years, much of the breeding range of Greenland White-fronted Geese has been invaded by Atlantic Canada Geese *Branta canadensis* originating from the Ungava Peninsula of northern Quebec (Fox *et al.* 1996; Kristiansen *et al.* 1999; Malecki *et al.* 2000; Scribner *et al.* 2003). Although most Canada Geese do not arrive until after the White-fronted Geese have begun to nest, they are behaviourally dominant over them in summer. During flightless moult, both species are constrained to feed near the safety of open water to escape predators. This is therefore a period when food supply may become limiting. Studies of moulting White-fronted Geese have shown them to forage on poorer quality diets in sympatry compared to allopatry (Kristiansen & Jarrett 2002). These observations led Fox *et al.* (2006) to suggest inter-specific competition in summer as the most likely cause of the recent decline of Greenland White-fronted Geese, although over large areas of the Canadian Arctic mainland and in Alaska the two species seem to co-exist quite successfully (e.g. Carriere *et al.* 1999).

Field observations of the age-composition of flocks in wintering areas after the geese have completed their autumn migration cannot provide reliable means of choosing between alternative explanations of variations in breeding success. Nevertheless, it seems likely that heavy spring snow cover has contributed to poor reproduction in some recent years. The former positive relationship between warm summers and reproductive output seems no longer to apply. However, the decline in reproductive output started in the mid 1980s, and in some recent years reproduction has been poor even when spring snow cover has been light, hence other contributory factors (*i.e.* other than meteorological variables) seem likely to be involved. The greater inhibition of reproduction amongst the birds wintering at Wexford than among those wintering on Islay in recent years may be significant. Wexford-wintering birds are known to breed further north in Greenland, staging internally within that country and starting to nest later (Kampp *et al.* 1988; Glahder *et al.* 1999a; Fox *et al.* 2003). These factors may make these birds even more susceptible to effects of heavy snow in spring. Northern-breeding geese may also be more at risk from interactions with greater concentrations of Canada Geese, particularly during the moult.

The effects of climate dealt with here have been incremental – the Atlantic Multidecadal Oscillation is, as the name suggests, slow-moving. Recent climate changes in the Northern Hemisphere are also speeding up melting of the Greenland ice sheet and consequent runoff (Hanna *et al.* 2008; Joughin *et al.* 2008), with dramatic examples of rapid discharge (Das *et al.* 2008). If the western margin of the ice sheet retreats eastward at increasing speed, as these studies suggest, the inland lowlands which are most favoured by Greenland White-fronted Geese will increase in extent and there will be changes in the composition of the vegetation at different altitudes. The changes are likely to be greatest in the low areas with organic soils that are preferred by the geese. These changes are likely to be helpful to the geese, though it is not yet possible to tell how quickly they may come about. Nor can we tell whether they will alter the comparative advantages that Canada Geese may now have over White-fronted Geese.

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